Polar Biol (2007) 30:369–378
DOI 10.1007/s00300-006-0193-7

ORIGINAL PAPER

The effects of forest fires on polar bear maternity denning habitat in western Hudson Bay

E. Richardson · I. Stirling · B. Kochtubajda

Received: 20 April 2005 / Revised: 11 July 2006 / Accepted: 20 July 2006 / Published online: 17 August 2006

Abstract The effects of forest fires on polar bear (*Ursus maritimus*) maternity denning habitat in western Hudson Bay were determined by comparing the physical characteristics of 48 burned and 101 unburned maternity den sites from September 2001 to October 2003. Fire significantly altered vegetation composition and increased the depth of the active layer, resulting in a decrease in the stability of den sites, the collapse of dens, and degradation of the surrounding habitat. Although bears investigated burned areas, analysis of mark and recapture data, satellite telemetry, radiotelemetry, and field observations all demonstrated that bears did not use burned areas for denning. While peat denning habitat is likely not limiting at this time, the re-use and occupancy of peat den sites during the summer may be an important means of energy conservation for pregnant female bears in western Hudson Bay. Increased energy expenditures in association with increased search times for suitable den sites and the excavation of new dens can potentially affect reproductive success. Predicted increases in forest fire activity as a result of climate change, along with the long-term recovery of denning habitat may reduce the amount of suitable denning habitat in the future. Resource managers need to be aware of the possibility of a shift in the distribution of denning bears and further loss of maternity denning habitat in western Hudson Bay.

E. Richardson (✉) · I. Stirling
Canadian Wildlife Service, 5320-122 St., Edmonton, AB, Canada T6H 3S5
e-mail: Evan.Richardson@ec.gc.ca

E. Richardson · I. Stirling
Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada R3T 2N2
e-mail: Ian.Stirling@ec.gc.ca

B. Kochtubajda
Meteorological Service of Canada, #200, 4999-98 Avenue, Edmonton, AB, Canada T6B 2X3
e-mail: Bob.Kochtubajda@ec.gc.ca

Introduction

Throughout most of their circumpolar range, pregnant female polar bears (*Ursus maritmus*) move on to land in late autumn to occupy maternity dens constructed in consolidated snowdrifts (Harington 1968; Uspenski and Ksitchinski 1972; Larsen 1985). At the southern portion of their range in western Hudson Bay, bears give birth to their young in late November and early December (Derocher et al. 1992) before the sufficient accumulation of snow for the construction of maternity dens (Scott and Stirling 2002). In this region, bears give birth to their young in dens dug into frozen peat banks which are later expanded into overlying snowdrifts sometime during the late winter (Jonkel et al. 1972; Ramsay and Stirling 1990; Clark et al. 1997). Unlike snow dens, earth dens in the permafrost remain as persistent landscape features and may be re-used by bears over several decades (Scott and Stirling 2002). Although detailed observations of bears excavating den sites have not been made, measurements and observations from within earthen dens indicate only limited excavation of permafrost at active den sites by female polar bears. It is believed that a significant energetic investment is likely required to excavate a den in

permafrost, promoting the re-use of existing dens in western Hudson Bay. Although den sites may be re-used, female bears in this region do not show fidelity to individual dens, but rather to general geographic areas (Ramsay and Stirling 1990). Protection of these areas becomes critical, as the maternal denning period is essential to the early development and survival of polar bear young (Blix and Lentfer 1979). Research indicates that disturbance of bears in maternal dens as a result of either natural or anthropogenic causes may lead to den relocation or abandonment of dens and reduced survival of young (Ramsay and Stirling 1986; Amstrup and Gardner 1994; Durner et al. 2003; Lunn et al. 2004).

For many mammals the availability of suitable den sites is an important factor affecting population recruitment (e.g., Russell 1983; Koopman et al. 1998; Norris et al. 2002; Fernández and Palomares 2000). The western Hudson Bay polar bear population contains approximately 950 individuals (Regehr et al. 2005, unpublished data) and an estimated 90% of the pregnant female bears in this population den in the area south of Churchill, Manitoba (Scott and Stirling 2002) accounting for the majority of recruitment in western Hudson Bay. The availability of suitable denning habitat is of particular importance to pregnant bears in this region, which have one of the longest fasting periods known for any mammal (Ramsay and Stirling 1988). Pregnant bears fast for up to 8 months while on land, using stored fat reserves to meet basic energetic demands as well as the increased energetic demands of gestation and lactation (Watts and Hansen 1987; Polischuk et al. 2001). In this region, pregnant bears begin to occupy dens in frozen peat banks 2–3 months in advance of parturition (Lunn et al. 2004, unpublished data), most likely as a means to escape warm ambient temperatures and conserve energy. Any significant loss of suitable den sites and/or denning habitat in this area could affect subsequent recruitment and the long-term viability of the western Hudson Bay polar bear population. The threat of habitat loss as a result of forest fires is a particular concern in the denning area. Between 1998 and 2003, several large fires burned through the western Hudson Bay denning area, disturbing extensive areas of denning habitat (Richardson 2004). Current research suggests that lightning strikes, the primary ignition source of fires in the Churchill area, will increase along with the frequency and extent of fires as a result of climatic warming (Flannigan and Van Wagner 1991; Price and Rind 1994; Flannigan et al. 1998, 2000). In addition, trends towards warmer spring air temperatures in the region (Skinner et al. 1998) could further extend the fire season. Collectively, these factors have the potential to significantly reduce the availability of suitable denning habitat in western Hudson Bay. Unlike anthropogenic disturbances (e.g., seismic activity around bear dens), which may be prevented or reduced through spatial and temporal modification of human activities (Amstrup and Gardner 1994), natural disturbances represent a greater challenge for resource managers as their dynamic nature precludes preventative measures in most situations.

Understanding the short-term and long-term impacts of forest fires on polar bear maternity denning habitat will be important to the conservation of the western Hudson Bay polar bear population. The objectives of the study were to examine (1) the impacts of forest fires on maternity denning habitat (2) to determine if female bears den in burned areas and (3) to examine the threat of habitat loss as a result of fire.

Methods

Study area

Our study area encompassed 2,200 km^2 in northeastern Manitoba near Churchill between 57°00′ and 58°50′N latitude and 92°25′ and 94°15′W longitude. Contained within this area is one of the most highly concentrated polar bear maternity denning areas in the world, much of which is protected by Wapusk National Park. The area consists of an extensive peatland located in the broad transition zone between the boreal forest and the arctic tundra (Ritchie 1960; Brook 2001). Much of the region is underlain by continuous permafrost, resulting in poor drainage and extensive bogs and fens (Brook 2001). Inland areas are characterized by open lichen tundra, with numerous lakes and small tundra ponds. Forest cover, primarily black spruce (*Picea mariana*), white spruce (*P. glauca*) and larch (*Larix laricina*) is most common in riparian areas along the edge of lakes, rivers and streams. Coastal areas are flat and dominated by sedge meadows (*Carex* spp.), salt marshes and interspersed relict beach ridges.

Locating burned dens

Surveys were conducted in known burned areas to locate dens that were impacted by fire. Den sites were located and sampled opportunistically between mid-August and early October 2001–2002 while flying in a Bell 206B helicopter during surveys for polar bears, as part of a long-term population study. Den sites located before this study that were known to be in areas that had been burned were also visited. Burned dens were

measured for the same physical and site level characteristics as undisturbed dens in order to investigate the impacts of fire.

The slope along the face of the bank at each den site was measured using an inclinometer. Vegetation composition was assessed visually as the percent cover of each plant species in a $10 \times 10\ m^2$ plot centered over top of the den site. Plant species were further grouped (tree, shrub, herb, lichens, and moss), un-vegetated areas were classified as bare ground and any burned vegetation was classified as burned. Although vegetation changes with time since disturbance, we did not attempt to further separate burned and unburned sites into different age classes. Physical characteristics recorded included depth to permafrost and substrate stability. Depth to permafrost (i.e., the active layer) was measured at three locations for each den (1) inside the den along the back wall (2) behind the den along the top of the bank and (3) along either side of the den along the bank using a steel permafrost probe. To obtain an index of substrate stability as it might be experienced by a bear seeking a den we used an improvised "clawometer" (see Holcroft and Herrero 1984). We measured the maximum pull (in kilograms) required to break the substrate surface using a short handled four tined garden rake attached to a 120 kg scale pulled parallel to the substrate surface. The tines on the rake were pushed straight down into the ground so that the handle was flat on the substrate surface. The scale was then attached to the end of the handle and pulled parallel to the ground until the rake broke free at which time the maximum pull in kilograms was measured. The physical state of each den was classified as stable (roof in tact; no slumping of den structure), slumping (slumping of roof or other portions of the den structure) or collapsed (collapse of the roof or collapse of other portions of the den structure).

Denning in burned areas

To determine the effects of forest fires on denning activity in specific portions of the denning area, a comparison between pre- and post-fire use of a large burn in the central portion of the denning area was made. The burn (hereafter referred to as the Lee Lake burn) occurred in July 1999 and burned 187 km^2 of habitat resulting in the largest known loss of polar bear denning habitat as a result of fire as of the 2003 fire season. This area was selected for more detailed analysis as it has been surveyed annually over the past 20 years as part of a long-term population monitoring program, providing pre-disturbance data. A comparison site of equal size and configuration was selected at Fletcher Lake, an area that has received similar amounts of survey effort over the same time period, but had not been impacted by fire. A global positioning system (GPS) was used to track flight routes to quantify survey effort in terms of total kilometers flown in disturbed and undisturbed habitats. To determine if bears make use of these areas for denning, the number of independent adult female bears (i.e., bears >5 years of age without accompanying young) captured from 1984 to 2003 during the fall sampling period were compared between the pre- and post-fire periods in the Lee Lake burn and the Fletcher Lake comparison site. Free ranging female bears were immobilized using standard capture protocols outlined by Stirling et al. (1989). While conducting surveys, additional observations of bears observed but not handled in burned areas were also recorded.

Use of burned versus adjacent unburned areas was further examined using bear movement data from Argos satellite collars (collected from 1991 to 1998). A total of 19 females were outfitted with radio collars, which were used to evaluate movements inside and outside known burned areas. In the summer and fall collars transmitted for a 6-h period every second day while female bears selected and entered maternity dens. Lunn et al. (2004) provide detailed information on collar deployment and filtering algorithms used for satellite locations. Satellite locations were imported into ArcView GIS software (Version 3.2, Environmental Systems Research Institute, Redlands, CA, USA) and movement data were superimposed over known burned areas. Burned areas were determined to be used if individual satellite locations occurred within the boundary of a burn. As a final means to address the use of burned areas by adult female bears, we examined habitat associations of 462 radio telemetry locations collected from VHF collars deployed on adult female bears from 1980 to 2004, to determine if any females irrespective of reproductive status were previously radio-located in burned areas.

Fire and lightning data

Burned areas (i.e., burn polygons) were identified using hotspot data provided by the Northern Forestry Centre in conjunction with the Canadian Wildland Fire Information System (CWFIS) (Lee 1995) and the Fire M3 program (Englefield et al. 2004). In addition, fire boundary maps (1970–1997) outlining the extent of burned areas were obtained from Manitoba Department of Conservation. Data were collected on all positive and negative cloud-to-ground lightning strikes detected in the study area from April to September for 1998–2003, to obtain an index of the frequency of the primary igni-

tion source of fires in the study area. Lightning data were collected by the Meteorological Service of Canada using IMPACT ES and LPAT sensors operating in northern Manitoba. Burrows et al. (2002) provide detailed information on the operation of the Canadian Lightning Detection Network. The frequency of lightning strikes was summarized on a yearly basis.

Habitat loss

The extent of habitat loss as a result of forest fires was determined using a denning habitat model (see Richardson et al. 2005) developed using resource selection functions (Manly et al. 1993) and forest fire data. Burned area polygons were overlain on the denning habitat map and the total number of pixels of suitable denning habitat within each polygon was calculated. Suitable denning habitat was considered to be any habitat that had a relative probability greater than 0.25 on a standardized scale from 0 to 1, where 1 is greatest relative probability of occurrence and 0 is the least. We chose a value of 0.25 so our estimate would most likely represent the maximum amount of habitat lost to fire. Habitat loss was assessed as the total loss of suitable denning habitat, as defined above, within a burned area measured in square kilometres.

Statistics

Habitat characteristics were tested for normality using Shapiro–Wilks tests. Features of burned and unburned den sites were compared using Mann–Whitney *U* tests as habitat characteristics were highly skewed and could not be normalized using standard transformation techniques. A *G* test was used to test for differences between the physical state of burned and un-burned dens. All tests were considered significant at a *P*-value of 0.05. Inferential statistics could not be used to analyze survey data from the study burn and control area due to issues with temporal autocorrelation of the survey data (see Hurlbert 1984). Therefore, summary statistics were used to describe observed differences in denning activity. All statistical analyses were conducted using SPSS (version 8.0, 1998).

Results

Den site characteristics

Several site level habitat characteristics at burned dens differed significantly from un-burned dens including vegetation cover, active layer depth, substrate stability, and the physical state of dens. Burned den sites had significantly less tree, herb and lichen cover than unburned den sites (Table 1). There were no significant differences in the percent cover of shrubs, moss or bare ground between burned and unburned sites (Table 1). Vegetation cover at burned den sites was limited and consisted primarily of herb, shrub cover and burned vegetation. Permafrost characteristics also varied significantly between sites. The active layer at un-burned dens was greatest at the side of the dens, less at the top of the banks, and was the least inside dens (Table 1). Similarly, the active layer at burned dens was greatest along the side of dens, slightly less along the top and least inside the den (Table 1). Burned den sites showed significantly deeper active layers than un-burned dens at the top, side and inside of the dens (Table 1). Mean substrate stability on top of un-burned dens was significantly greater than that of burned den sites. Similarly, substrate stability along the side of dens was significantly less for burned dens than un-burned dens. However, there was no significant difference in substrate stability inside burned and unburned dens (Table 1).

The physical state (stable, slumping or collapsed) of burned ($n = 48$) and un-burned ($n = 101$) dens was significantly different (*G*-test $\chi^2 = 42.78$, $df = 2$, $P < 0.001$).

Table 1 Permafrost stability, active layer thickness, substrate stability and ground cover at burned and unburned polar bear (*Ursus maritimus*) den sites in the Churchill region of Manitoba

Den characteristics	Burned den ($n = 48$)	Un-burned den ($n = 101$)	*P*
Active layer top (cm)	54.1 ± 8.8 (54)	35.2 ± 9.1 (31)	<0.001
Active layer side (cm)	78.3 ± 13.1 (76.5)	49.3 ± 15.3 (38.5)	<0.001
Active layer inside (cm)	41.8 ± 11.2 (38)	23.3 ± 6.3 (21)	<0.001
Stability top (pull kg)	33.0 ± 7.8 (30)	48.1 ± 11.3 (46)	<0.001
Stability side (pull kg)	27.8 ± 9.3 (25)	44.3 ± 11.5 (41)	<0.001
Stability inside (pull kg)	12.2 ± 4.2 (10)	12.9 ± 5.2 (10)	0.876
Tree (%)	1.8 ± 5.0 (0)	29.2 ± 16.0 (30)	<0.001
Shrub (%)	18.1 ± 12.4 (11)	17.9 ± 11.3 (13)	0.358
Herb (%)	11.6 ± 8.5 (11)	16.7 ± 11.5 (13)	0.003
Moss (%)	4.0 ± 5.7 (1)	7.4 ± 10.3 (1)	0.187
Lichen (%)	8.6 ± 13.5 (2)	27.5 ± 16.4 (30)	<0.001
Ground (%)	8.8 ± 9.8 (10)	7.0 ± 7.3 (10)	0.770
Burned (%)	51.9 ± 31.2 (65)	0.0 ± 0.0 (0)	<0.001

Note: Values are means ± standard deviation (median)

Den sites that had been burned were much more susceptible to collapse with 66% of all burned dens collapsing compared to only 23% of un-burned dens. Burned and un-burned dens had equal amounts of slumping (32%). Comparatively, 46% of unburned dens were stable ($n = 46$) while only 2% ($n = 1$) or 1 burned den was stable (see Figs. 1, 2).

Denning in burned areas

Observations after the Lee Lake burn in 1999 indicated that bears initially returned to the area and excavated a number of shallow dens primarily in the first year after the fire, as of 2004 no bears have been observed denning in the area since the fire. Mark and recapture records indicate an average of 1.4 ± 0.5 (SE), 2.4 ± 0.8, and 1.8 ± 0.9 independent female bears were handled within the bounds of the Lee Lake burn each year during the periods from 1984–1988, 1989–1993 to 1994–1998, respectively, before the fire occurred. In the 5 years since the Lee Lake burn (1999–2003), no bears have been handled and only one bear was sighted in the burn. Mark and recapture data from the control area during the periods of 1984–1988, 1989–1993 and 1994–1998 indicate an average of 7.2 ± 1.6, 9.2 ± 1.4, and 10.0 ± 1.2 bears were handled each year respectively. In the 5 years since the Lee Lake burn (1999–2003) an average of 5.2 ± 3.4 bears have been handled in the Fletcher Lake comparison site. Comparatively over the same time period there has been almost complete absence of activity in the Lee Lake burn. GPS mapping of flight routes indicated a total of 1,053 km were flown in the Lee Lake burn from 2001 to 2003 and was comparable with 1,010 km of habitat surveyed in the Fletcher Lake site during the same time period. During surveys of burned areas only two bears were observed in burned denning habitat, neither of which had successfully excavated a den.

Fig. 1 Typical polar bear maternity den site along the edge of a lake in Wapusk National Park. (A.) Excavated peat from den (B.) vegetated bank habitat along the edge of a lake and (C.) krummholz spruce characteristic of most den sites

Fig. 2 Burned maternity den site in Wapsuk National Park showing the removal of vegetation and subsequent collapse of the den as a result of fire. (A.) Old den chamber (B.) collapsed roof and (C.) slumping of bank habitat

Seven hundred and ninety-six onshore locations were obtained from the 19 female bears fitted with satellite collars. Only two bears transmitted locations from inside identified burned areas. The 2 bears were located 11 and 8 times, respectively in burned areas. In the fall of 1997, one of the females which was known to be pregnant spent 53 days in a burn, but subsequently left the burn to den in an unburned area. This particular female bear was re-sighted with two cubs of the year in the fall of 1998, indicating that she had successfully denned the previous year. The second female bear spent an estimated 15 days in burned areas from 20 August to 8 November in 1997 but made no attempt to den in 1997 and returned to the sea ice the same fall. As a final means to investigate the use of burned areas we examined habitat associations of 462 VHF locations collected over the last 24 years. Observations of the habitat type systematically recorded for all radio-collar locations indicated no female bears had been radio-located in burned areas during this period.

Fire and climate data

From 1998 to 2003, 36,330 lightning strikes were detected in the study area. The average number of strikes per year was $6{,}055 \pm 2{,}648$ (SD) and ranged from 2,896 to 9,734 (see Table 2). During the fire

Table 2 Frequency of lightning strikes, forest-tundra fires, total area burned and potential loss of polar bear maternity denning habitat in the Churchill region of Manitoba from 1998 to 2003

Year	Number of lightning strikes	Number of burns	Area burned (km^2)	Potential habitat loss (km^2)
1998	2,896	3	25.70	2.03
1999	5,176	18	683.73	46.08
2000	4,253	6	31.43	0.42
2001	5,521	0	0.00	0.00
2002	8,750	0	0.00	0.00
2003	9,734	6	204.03	18.63
Total	36,330	33	944.89	67.16

season the majority of lightning strikes were restricted to isolated events that lasted from 1 to 2 days (e.g., on July 23rd and 24th of 2003 1,986 and 2,306 strikes were recorded, respectively; representing 44% of all lightning strikes in 2003).

Detected forest-tundra fires varied in both frequency and extent between years. Fires were recorded in 1998, 1999, 2000 and 2003 (Table 2). No fires were observed in 2001 or 2002. The total areas burned in 1998, 1999, 2000 and 2003 was 28, 683, 31, and 204 km^2, respectively. It is important to note, that although smaller fires (<1 km^2 in area) were not detected in this study, it is acknowledged that large fires account for the majority (~97%) of the total area burned in Canada (Stocks et al. 2003) and therefore we feel that the fires detected in this study likely represent the majority of the area burned in the study area from 1998 to 2003.

Habitat loss

Using the classification scheme for suitable denning habitat outlined in the methods and the denning habitat model from Richardson et al. (2005) an estimated 1,210 km^2 of suitable denning habitat existed in the study area in 1996. Within the 944 km^2 that burned in the study area over the last 6 years, 67 km^2 (approximately 5.5%) of the suitable polar bear denning habitat was impacted. The greatest habitat loss occurred in 1999 where 46 km^2 of denning habitat burned. In 1998, 2000 and 2003 denning habitat of 2, 0.5, and 18 km^2 of habitat was burned.

Discussion

Forest fires significantly impact polar bear maternity den sites and denning habitat by altering essential microhabitat requirements (i.e., vegetation cover, substrate stability and permafrost), resulting in the collapse of existing dens and the avoidance of burned areas by denning bears. Removal of vegetation, in particular tree cover, is the primary factor that led to the observed decreased stability of burned den sites. In addition to providing substrate stability, trees also facilitate the accumulation of snow over den sites in the winter (Scott and Stirling 2002). Pearson (1975) and Nagy et al. (1983) suggested that grizzly bears (*U. arctos*) construct dens directly underneath vegetation due to the increased accumulation of snow in the winter, which may help insulate den sites. Microenvironments 25–35 cm beneath the snow surface can be up to 22°C warmer than the surface air temperature (Pruitt 1957). Thus, the loss of this insulating layer may affect the warmth of the denning environment and also the availability of suitable snow drifts for bears to tunnel out into in the spring.

Degradation of permafrost as a result of fire has been well documented (Zoltai and Petapiece 1974; Thie 1974; Mackay 1995; Swanson 1996; Burn 1998). We found that fire significantly increased the active layer in burned areas through the removal of vegetation, which affects permafrost formation (Zoltai and Petapiece 1974; Mackay 1995). Melting of permafrost led to the slumping of banks, and decreased stability of denning habitat and den sites. At many burned den sites, large blocks of peat have broken free from the banks and slumped down slope (Fig. 2), as a result of the cumulative effects of the vegetation removal and the melting of permafrost. In addition to providing den site stability, the presence of permafrost also provides a cool microenvironment for pregnant female bears, allowing them to conserve energy and avoid warm ambient temperatures and insects in the summer (Jonkel et al. 1972). Permafrost degradation in burned areas, in association with black substrates, which absorb significantly more solar radiation (Wein and Bliss 1973), will presumably result in warmer microclimates, which may be unfavorable for bears. As a consequence of continued climatic warming, Gough and Leung (2002) suggested there is likely to be significant permafrost degradation in the Hudson Bay region over the next 50 years. Continued degradation of permafrost and slumping of banks is likely to further reduce the amount of suitable denning habitat in western Hudson Bay.

A benefit of permafrost degradation may be an increase in the ease with which den sites are excavated. Hammer (1999) noted that grizzly bears appear to have difficulty digging in frozen ground, even with their long claws, which are an adaptation to digging (Derocher and Stirling 1990). Presumably, polar bears experience similar difficulties in excavating frozen ground/peat at

den sites. Observations from within recently active den sites indicate that polar bears do not extensively excavate permafrost, resulting in partially excavated dens. We suggest that in most areas where permafrost is close to the surface, the construction of dens may occur over several years as the permafrost subsides and bears are able to dig further into the bank. The significant amount of time and energy likely required to establish a suitable den site may explain the long-term re-use of dens over several decades documented by Scott and Stirling (2002).

Use of burned areas by bears

The effects of natural (e.g., forest fires) and accidental anthropogenic disturbances (e.g., oil spills) cannot be studied using well-replicated randomized study designs because they are unplanned and for ethical reasons cannot normally be replicated. As a result statistical analysis of the impacts of these disturbances suffer from problems of confounding and temporal autocorrelation (Eberhardt and Thomas 1991; Weins and Parker 1995). Despite these difficulties it is important that resource managers attempt to quantify the impacts of these types of disturbances. We were fortunate to have both pre- and post-disturbance data to examine the use of a burn by female bears that occurred over a substantial amount of high quality maternity denning habitat in our study area. We observed that some pregnant female bears returned to the burned area after the fire and investigated potential den sites. However, there was no evidence that any of these bears denned in the burned areas. Even though the number of active dens in different parts of the study area can vary between years, the decline in denning activity (i.e., number of bears observed) in the burned area in the 5 years following the Lee Lake fire indicates that burned areas are not suitable for denning. Furthermore, because bears are more easily spotted in burned areas, the number of bears observed and captured in the area of the Lee Lake burn before the fire is likely a conservative estimate of the actual number of bears that may have previously used this area.

Previous shifts in the distribution of denning female polar bears and the location of their dens have been attributed to changes in the availability of snowdrifts and ice conditions which limit access to terrestrial denning areas (Harington 1968; Lønø 1970; Schweinsburg et al. 1984). Similarly, changes in the distribution of suitable denning habitat as a consequence of fire will likely result in shifts in the location of den sites and female bears in the denning area. Female bears in western Hudson Bay show fidelity to certain portions of the denning area (Ramsay and Stirling 1990; Scott and Stirling 2002). However, our study indicates that while female bears may return to burned areas, likely because of previously denning there, they do not appear to continue to show fidelity to these areas. Presumably, investigation of burned areas along with subsequent relocation and establishment of a maternity den elsewhere will require increased energy expenditure by individual female bears. In western Hudson Bay, decreased reproductive success in adult female polar bears was linked with decreases in the body mass (Derocher and Stirling 1995), thus any significant increase in energy expenditure prior to den occupation could affect reproductive success. Female bears in western Hudson Bay begin to occupy dens as early as August (Lunn et al. 2004) up to 3 months prior to giving birth in late November and early December (Derocher et al. 1992). This extended period of den occupancy is an important means of escaping warm ambient temperatures and conserving energy further highlighting the importance of these reproductive sites.

Climate change and forest fires

Understanding the dynamics of forest fires is important in trying to assess the potential for habitat loss in our study area. Because lightning starts almost all of the fires in our study area, we examined the frequency of lightning strikes to get an estimate of the number of ignition sources throughout the study area each summer. Lightning activity is predicted to increase as a result of climate change and with the greatest increases happening in the northern hemispheres in the summer (Price and Rind 1994), when the majority of fires occur in our study area. Along with this are predictions of warming summer temperatures in our study area (Suffling and Scott 2002), which may result in more favorable conditions for fires (see Flannigan et al. 2005) such as those in 1999 in our study area. In addition, Skinner et al. (1998) suggest a warming trend in spring temperatures, which could result in a longer fire season. Taken together these data suggest a serious potential for increased fire activity and habitat loss.

Maternity denning habitat may be particularly susceptible to fire as resinous shrubs (i.e., krummholtz spruce over top of dens) are more flammable than other fuel sources (e.g., graminoids) (Auclair 1983) and the peat substrate in which bears den is readily burned. Although forest fires tend to vary widely in both intensity and frequency (Heinselman 1973; Bergeron et al. 2004), burns in denning habitat appeared to burn slowly and intensely as indicated by penetration of the peat layer and subsequent burning of the

root mat of trees at den sites (Fig. 2). The spruce krummholz found over top of most dens largely spread by leaders and do not produce large amounts of viable seeds (Black and Bliss 1980; Payette and Gagnon 1985) which may inhibit the re-establishment of spruce after fire (Arsenault and Payette 1992). Arsenault and Payette (1992) noted that a reduction in the accumulation of snow in these areas, ultimately as a result of fire, lead to the succession of lichen tundra vegetation, which may further limit the establishment of black spruce (Morneau and Payete 1989). Scott and Stirling (2002) reported that krummholz spruce above den sites may be in excess of 230 years old, indicating that even if spruce reestablish after fire, the regeneration times may be extensive. Although the amount of suitable denning habitat in the study area does not appear to be limited at present, increased fire frequency and slow succession rates back to suitable denning habitat or changes in successional trajectories could affect the future distribution and availability of denning habitat for bears in the region.

When considering the impacts of habitat loss it is important to assess how much denning habitat would be required to support the 150–200 bears, which are estimated to den in this area annually (see Derocher and Stirling 1995). Dens were found in much higher densities in localized areas of Svalbard (Bogen Valley 12.5 dens/km^2) (Larsen 1985) and on Herald I. (Main Valley 12.1 dens/km^2 (Osyanikov 1998). Several locations in the study area support large numbers of dens, so it is likely that a relatively limited amount of denning habitat would still be adequate to support this population. An important caveat to this is that as the number of dens and amount of denning habitat decreases, the energetic expenditures of adult female bears will likely increase.

The long-term impacts of climatic warming and forest fire activity on maternity denning habitat remain unknown. However, because of increased rates of den collapse in burned areas, decreased stability of denning habitat, and long recovery times, any increase in the frequency or extent of forest fires will likely result in a reduction in the number of dens and amount of suitable denning habitat. Mangers must consider the long term impacts of a significant increase in the persistence of this natural disturbance and evaluate where fire suppression would be appropriate to preserve polar bear maternity denning habitat in western Hudson Bay.

Acknowledgments We wish to thank Parks Canada, Canadian Wildlife Service, World Wildlife Fund Canada, Polar Bears International, Natural Science and Engineering Research Council (Ian Stirling), Northern Science Training Program, University of Alberta and the Churchill Northern Studies Centre for providing financial support to this project. D. Andriashek, N. Lunn, S. Sutton, K. Burke, J. Henderson all provided assistance in the field. R. Brook provided access to the Wapusk National Park vegetation map and the original satellite imagery. N. Lunn provided valuable comments on the initial manuscript. We thank Andy Derocher and one anonymous reviewer for their constructive criticism, which improved the overall quality of the manuscript.

References

Amstrup SC, Gardner C (1994) Polar bear maternity denning in the Beaufort Sea. J Wildl Manage 58:1–10

Arsenault D, Payette S (1992) A postfire shift from lichen-spruce to lichen-tundra vegetation at tree line. Ecology 73:1067–1081

Auclair AND (1983) The role of fire in lichen-dominated tundra and forest-tundra. In: Wein RW, MacLean DA (eds) The role of fire in northern circumpolar ecosystems. Wiley, New York

Bergeron Y, Flannigan M, Gauthier S, Leduc A, Lefort P (2004) Past, current and future fire frequency in the Canadian Boreal Forest: implications for sustainable forest management. Ambio 33:356–360

Black RA, Bliss LC (1980) Reproductive ecology of *Picea mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecol Monogr 50:331–354

Blix AS, Lentfer JW (1979) Modes of thermal protection in polar bear cubs at birth and on emergence from the den. Am J Physiol 263:67–74

Brook RK (2001) Structure and dynamics of the vegetation in Wapusk National Park and the Cape Churchill Wildlife Management Area of Manitoba: community and landscape scales. M.N.R.M. thesis, Natural Resource Institute, The University of Manitoba, Winnipeg

Burn CR (1998) The response (1958–1997) of permafrost and near-surface ground temperatures to forest fire, Takhini River valley, southern Yukon Territory. Can J Earth Sci 35:184–199

Burrows WR, King P, Lewis PJ, Kochtubajda B, Snyder B, Turcotte V (2002) Lightning occurrence patterns over Canada and adjacent United States from lightning detection network observations. Atmos Ocean 40:59–81

Clark DA, Stirling I, Calvert W (1997) Distribution, characteristics, and use of earth dens and related excavations by polar bears on the western Hudson Bay lowlands. Arctic 50:158–166

Derocher AE, Stirling I (1990) Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Can J Zool 68:1395–1403

Derocher AE, Stirling I (1995) Estimation of polar bear population size and survival in western Hudson Bay. J Wildl Manage 59:215–221

Derocher AE, Stirling I, Andriashek D (1992) Pregnancy rates and serum progesterone levels of polar bears in western Hudson Bay. Can J Zool 70:561–566

Durner GM, Amstrup SC, Fischbach A (2003) Habitat characteristics of polar bear terrestrial maternal den sites in northern Alaska. Arctic 56:55–62

Eberhardt LL, Thomas JM (1991) Designing environmental field studies. Ecol Monogr 61:53–73

Englefield P, Lee BS, Fraser RH, Landry R, Hall RJ, Lynham TJ, Cihlar J, Li Z, Jin J, Ahern FJ (2004) Applying geographic information systems and remote sensing to forest fire monitoring, mapping, and modeling in Canada. In: Engstrom RT,

Galley KEM, deGroot WJ (eds) Proceedings of the 22nd tall timbers fire ecology conference: fire in temperate, boreal, and montane ecosystems. Tall Timbers Research Station, Tallahassee, pp 240–245

Fernández N, Palomares F (2000) The selection of breeding dens by the endangered Iberian lynx (*Lynx pardinus*): implications for its conservation. Biol Conserv 94:51–61

Flannigan MD, Van Wagner CE (1991) Climate change and wildfire in Canada. Can J For Res 21:66–72

Flannigan MD, Bergeron Y, Englemark O, Wotton BM (1998) Future wildfire in circumboreal forest in relation to global warming. J Veg Sci 9:469–476

Flannigan MD, Stocks BJ, Wotton BM (2000) Climate change and forest fires. Sci Total Environ 262:221–229

Flannigan MD, Logan KA, Amiro BD, Skinner WR, Stocks BJ (2005) Future area burned in Canada. Clim Change (in press)

Gough WA, Leung A (2002) Nature and fate of Hudson Bay permafrost. Reg Environ Change 2:177–184

Hammer D (1999) Forest fires influence on yellow hedysarum habitat and its use by grizzly bears in Banff National Park, Alberta. Can J Zool 77:1513–1520

Harington CR (1968) Denning habits of the polar bear (*Ursus maritimus* Phipps). Canadian Wildlife Service Report Series No. 5, 30 p

Heinselman ML (1973) Fire in the virgin forests of the Boundary Waters Canoe Area. Minnesota Quat Res 3:329–382

Holcroft AC, Herrero S (1984) Grizzly bear digging sites for *Hedysarum sulphurescens* roots in southwestern Alberta. Can J Zool 62:2571–2575

Hurlbert SH (1984) Psuedoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211

Jonkel C, Kolenosky GB, Robertson RJ, Russell R (1972) Further notes on polar bear denning habits. Int Conf Bear Res Manage 2:142–158

Koopman ME, Scrivner JH, Kato TT (1998) Patterns of den use by San Joaquin kit foxes. J Wildl Manage 51:606–616

Larsen T (1985) Polar bear denning and cub production in Svalbard, Norway. J Wildl Manage 49:320–326

Lee BS (1995) The Canadian wildland fire information system. In: Proceedings of the 9th annual symposium on geographic information systems in forestry, environment and natural resource management. GIS World, Fort Collins, pp 639–646

Lønø O (1970) The polar bear (*Ursus maritimus* Phipps) in the Svalbard area. Norsk Polarinstitutt Skrifter 149:1–115

Lunn NJ, Stirling I, Andriashek D, Richardson E (2004) Selection of maternity dens by female polar bears in western Hudson Bay. Polar Biol 27:350–356

Mackay JR (1995) Active layer changes (1968 to 1993) following the forest-tundra fire near Inuvik, N.W.T., Canada. Arct Alp Res 27:323–336

Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London

Morneau C, Payete S (1989) Post-fire lichen-spruce woodland recovery at the limit of the boreal forest in northern Québec. Can J Botany 67:2770–2782

Nagy JA, Russell RH, Pearson AM, Kingsley MCS, Larsen CB (1983) A study of grizzly bears on the Barren Grounds of Tuktoyaktuk Peninsula and Richards Island, Northwest Territories, 1974 to 1978. Canadian Wildlife Service Edmonton, Alberta

Norris DR, Theberge MT, Theberge JB (2002) Forest composition around wolf (*Canis lupus*) dens in eastern Algonquin Provincial Park Ontario. Can J Zool 80:866–872

Osyanikov N (1998) Den use and social interactions of polar bears during spring in a dense denning area on Herald Island, Russia. Ursus 10:251–258

Payette S, Gagnon R (1985) Late Holocene deforestation and tree regeneration in the forest-tundra of Québec. Nature 313:570–572

Pearson AM (1975) The northern Interior grizzly bear *Ursus arctos* L. Can Wildl Serv Rep Ser 34:86

Polischuk SC, Hobson KA, Ramsay MA (2001) Use of stable-carbon and—nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. Can J Zool 79:499–511

Price C, Rind D (1994) Possible implications of global climate change on global lightning distributions and frequencies. J Geophys Res 99:823–831

Pruitt WO (1957) Observations on the bioclimate of some taiga mammals. Arctic 10:131–138

Ramsay MA, Stirling I (1986) On the mating system of polar bears. Can J Zool 64:2142–2151

Ramsay MA, Stirling I (1988) Reproductive biology and ecology of female polar bears (*Ursus maritimus*). J Zool Lond 214:601–634

Ramsay MA, Stirling I (1990) Fidelity of female polar bears to winter den sites. J Mammal 71:233–236

Regehr E, Lunn NJ, Amstrup SC, Stirling I (2005) Population decline of polar bears in Western Hudson Bay in relation to climatic warming. In: 16th biennial conference on the biology of marine mammals, San Diego, California, 12-16 December 2005. Society for Marine Mammalogy, p 233 (Abstract only)

Richardson E (2004) Polar bear (*Ursus maritimus*) maternity den site selection and the effects of forest fires on denning habitat in western Hudson Bay. M.Sc Thesis, Department of Biological Sciences, University of Alberta, Edmonton

Richardson E, Stirling I, Hik DS (2005) Polar bear (*Ursus maritimus*) maternity denning habitat in western Hudson Bay: a bottom up approach to resource selection functions. Can J Zool 83:860–870

Ritchie JC (1960) The vegetation of northern Manitoba V. Establishing the major zonation. Arctic 13:211–229

Russell, RH (1983) Swift fox. In: Hinterlands Who's Who. Canadian Wildlife Service, Environment Canada, Ottawa

Schweinsburg RE, Spencer W, Williams D (1984) Polar bear denning area at Gateshead Island, Northwest Territories. Arctic 37:169–171

Scott PA, Stirling I (2002) Chronology of terrestrial den use by polar bears in western Hudson Bay as indicated by tree growth anomalies. Arctic 55:151–166

Skinner WR, Jefferies RL, Carleton TJ, Rockwell RF, Abraham KF (1998) Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. Glob Chan Biol 4:3–16

SPSS Inc. (1998) SPSS®. Version 8.0 [computer program]. SPSS-Inc., Chicago

Stirling I, Spencer C, Andriashek D (1989) Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arcitc. J Wildl Dis 25:159–168

Stocks BJ, Mason JA, Todd JB, Bosch EM, Wotton BM, Amiro BD, Flannigan MD, Hirsch KG, Logan KA, Martell DL, Skinner WR (2003) Large forest fires in Canada, 1959–1997. J Geophys Res 107:1–12

Suffling R, Scott D (2002) Assessment of climate change effects on Canada's national park system. Environ Monit Assess 74:117–139

Swanson DK (1996) Susceptibility of permafrost soils to deep thaw after forest fires in interior Alaska, U.S.A., and some ecological implications. Arct Alp Res 28:217–227

Thie J (1974) Distribution and thawing of permafrost in the southern part of the discontinuous permafrost zone in Manitoba. Arctic 27:189–200

Uspenski SM, Kistchinski AA (1972) New data on the winter ecology of the polar bear (*Ursus maritimus*) on Wrangel Island. IUCN (Int Union Conserv Nat Nat Resour) Publ New Ser 23:181–197

Watts PD, Hansen SE (1987) Cyclic starvation as a reproductive strategy in the polar bear. Symp Zool Soc Lond 57:305–318

Wein RW, Bliss LC (1973) Change in arctic *Eriophorum* tussock communities following fire. Ecology 54:845–852

Weins JA, Parker KA (1995) Analyzing the effects of accidental environmental impacts: approaches and assumptions. Ecol Appl 5:1069–1083

Zoltai SC, Petapiece WW (1974) Tree distribution on perennially frozen earth hummocks. Arct Alp Res 6:403–411